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The biology of tiger sharks, *Galeocerdo cuvier*, in Shark Bay, Western Australia: sex ratio, size distribution, diet, and seasonal changes in catch rates

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Synopsis

Tiger sharks, *Galeocerdo cuvier*, are apex predators in a variety of nearshore ecosystems throughout the world. This study investigates the biology of tiger sharks in the shallow seagrass ecosystem of Shark Bay, Western Australia. Tiger sharks ($n = 252$) were the most commonly caught species (94%) compared to other large sharks. Tiger sharks ranged from 148–407 cm TL. The overall sex ratio was biased towards females (1.8 : 1), but the sex ratio of mature animals (> 300 cm TL) did not differ from 1 : 1. Contrary to previous accounts, tiger sharks were caught more often in all habitats during daylight hours than at night. Tiger shark catch rates were highly correlated with water temperature and were highest when water temperatures were above 19°C. The seasonal abundance of tiger sharks is correlated to both water temperature and the occurrence of their main prey: sea snakes and dugongs, *Dugong dugon*. Stomach contents analysis indicated that sea turtles and smaller elasmobranchs were also common prey. The importance of major seagrass grazers (dugongs and green sea turtles, *Chelonia mydas*) in the diet of tiger sharks suggests the possibility that these sharks are keystone predators in this ecosystem.

Introduction

Tiger sharks, *Galeocerdo cuvier*, are an apex predator in many tropical and warm-temperate ecosystems around the world (Randall 1992). Growing to sizes of 5.5 m, they are capable of consuming large-bodied prey, and have a highly varied diet that includes teleosts, elasmobranchs, birds, sea snakes, turtles, marine mammals, crustaceans, molluscs, and anthropogenic food sources (Randall 1992, Simpfendorfer 1992, Lowe et al. 1996, Simpfendorfer et al. 2001). Tiger sharks exhibit ontogenetic shifts in diet (Simpfendorfer 1992, Lowe et al. 1996) where small sharks tend to consume primarily fishes and sea snakes but, as they grow, sharks diversify their diet by including larger prey items (e.g. sea turtles and marine mammals). As one of the few predators on large marine animals, tiger sharks may influence prey species behavior and population sizes (Simpfendorfer et al. 2001, unpublished data).

Previous studies have demonstrated that there is geographic variation in the diets of tiger sharks, suggesting they are capable of taking advantage of locally abundant resources. In Hawaii, tiger sharks have a broad diet; teleost fishes make up a large portion of the diet of all size classes of sharks, and marine mammals and sea turtles are relatively uncommon, even in large sharks (Lowe et al. 1996). Sea birds are the most common prey item for tiger sharks in the northwestern Hawaiian islands (DeCrosta et al.[1]). In contrast, sea snakes are one of the most important prey items of tiger sharks in Queensland, Australia (Simpfendorfer 1992) and New Caledonia (Rancurel & Intes 1982). Finally, in Western

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[1] DeCrosta, M. A., L. R. Taylor Jr. & J. D. Parrish. 1984. Age determination, growth, and energetics of three species of carcharhinid sharks in Hawaii. pp. 75–95. *In*: Proceedings of the Second Symposium on Resource Investigations in the Northwestern Hawaiian Islands, vol. 2, University of Hawaii Sea Grant Miscelaneous Report 84-01.

Australian waters, turtles and marine mammals are two of the most common prey items found in tiger sharks, but even within Western Australia there is substantial geographic variation in diet (Simpfendorfer et al. 2001).

Tiger sharks are believed to migrate into higher latitudes during warm periods (Bigelow & Schroeder 1948, Stevens 1984, Randall 1992), but evidence for this is largely anecdotal. It is unclear whether these migrations are in response to thermal conditions and physiological constraints or are the result of changes in prey abundance or distribution. In general, the influence of prey availability on tiger shark movements has been overlooked although they can move relatively large distances (e.g. Kohler et al. 1998, Holland et al. 1999) and appear to take advantage of seasonally abundant food resources. For example, tiger sharks are only present in large numbers at the Houtman Abrolhos Islands, Western Australia, during the Western rock lobster fishing season when discarded bait is an abundant food source (Simpfendorfer et al. 2001).

The present study investigates the biology of tiger sharks in the seagrass ecosystem of Shark Bay, Western Australia. It describes the influence of fishing techniques on tiger shark catches, as well as tiger shark sex ratio, size distribution, diet, seasonal abundance and site fidelity. Finally, this study is the first to investigate the influences of water temperature and prey availability on tiger shark catch rates.

Methods and materials

Study site

Shark Bay is a large, semi-enclosed bay 800 km north of Perth, Western Australia (Figure 1a). The bay is relatively shallow throughout with extensive shallow seagrass banks (<4.0 m depth), numerous narrow, swift-current channels (6.5–12 m), and broad expanses of relatively deeper waters (6.5–15 m). Shark Bay contains the most extensive seagrass shoals reported in the world (Walker 1989) and supports a large population of tiger sharks that have not been subjected to commercial fishing pressure since 1994. Even before the 1994 commercial shark fishing ban, fishing pressure was from only a single operator whose efforts were focused in the Western Gulf (C. Simpfendorfer personal communication). The study site was located in the Eastern Gulf, offshore of the Monkey Mia Dolphin Resort (approx. 25°45′S, 113°44′E; Figure 1b). The habitats represented in the study area include seagrass shoals, channels, and open deep waters (Figure 1c).

Water temperature was measured at a consistent location (Figure 1c), 1 m below the surface, each day at 7:00 h. There was seasonal variation in water temperature within the study area (Figure 2). Water temperatures during warm months (September–May) were generally above 20°C but dropped as low as 14°C in winter months (June–August). Temperatures tended to drop rapidly in mid to late May, then increased gradually in late August. During cold months, water temperatures in the Western Gulf, and especially near Dirk Hartog Island, are considerably warmer due to a warm-water current (Cresswell 1991). For the purposes of this paper data from 1997 and 1998 were pooled due to similar thermal conditions. The data from 1999 are analyzed separately since winter temperatures were higher than those of 1997/1998. There are no differences in water temperature among habitats due to the generally shallow nature of the bay and to the water being well mixed by strong tidal currents and wind (unpublished data).

Study methods

Tiger sharks, as well as other large sharks, were captured using drumlines equipped with a single hook (Mustad Shark Hook size 12/0, 13/0, or 14/0) fished at a depth of 0.7–2.0 m. Up to ten lines, baited with approximately 2 kg of Australian salmon, *Arripis truttaceus*, were set at dawn or dusk in at least two zones (one shallow, one deep; Figure 1). Lines were spaced approximately 0.7 km apart and were checked every 2–4 hours. Bait presence/absence was noted on lines that did not catch sharks. Hook soak time was measured as the time from deployment until line removal. If bait was not present at a check, or a shark was caught, the bait was considered to be lost half way between the previous check (when bait was present) and the time when loss or a shark was detected.

During warm months, bait loss occurred more rapidly and at a much higher frequency in shallow habitats than in deep habitats, making it impossible to accurately measure differences in catch rates among habitats. Other factors, including potential differences in the effectiveness of odor corridors from baits and differing catch radii among habitats would make comparisons among habitats based on catch rates difficult to interpret. Therefore, habitat use by tiger sharks will not be addressed in this paper.

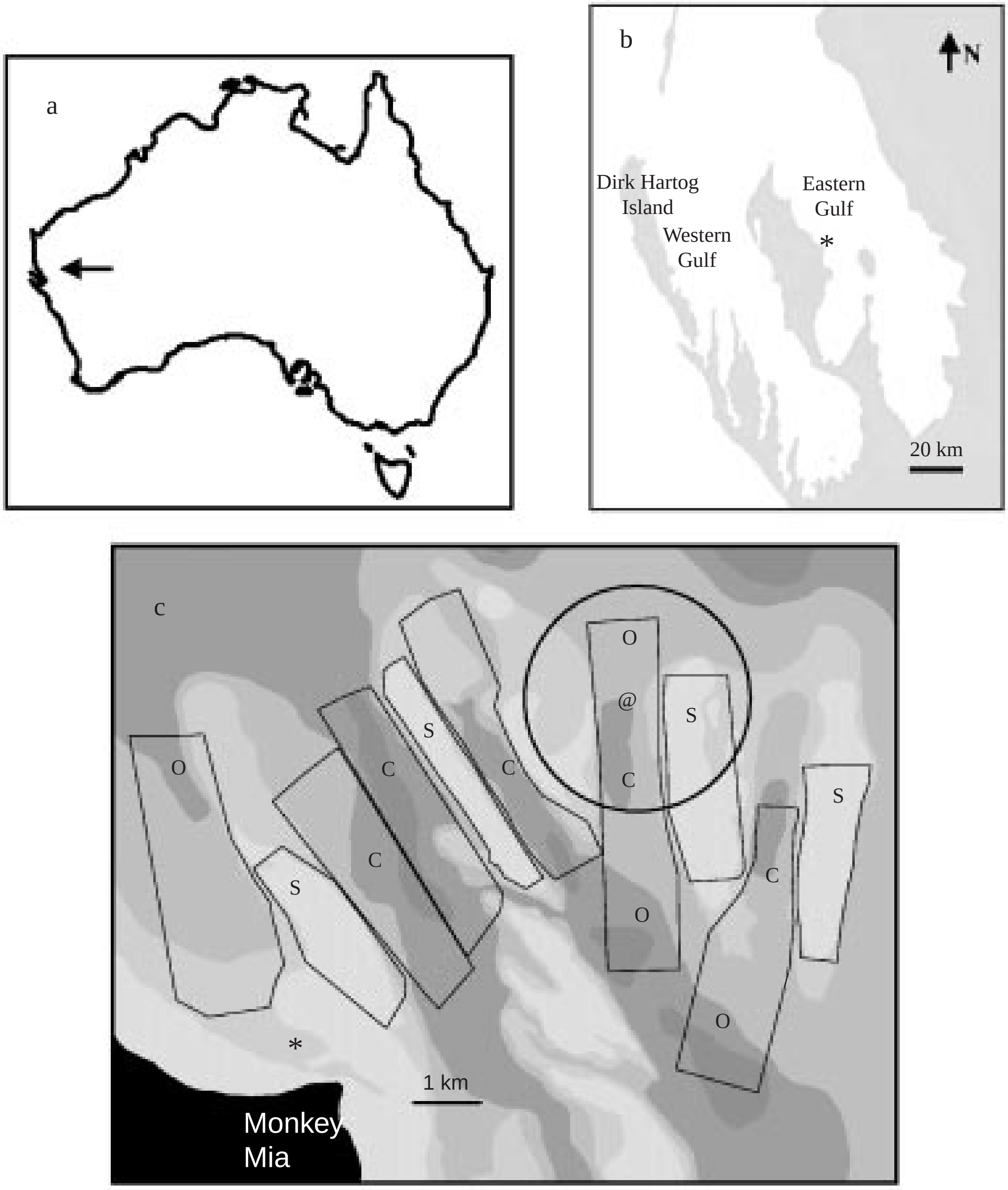

Figure 1. a – Shark Bay, Western Australia (indicated by arrow). b – The study area (∗) was located in the Eastern Gulf of Shark Bay. c – Study zones are represented by black polygons. Shark fishing was not conducted in the zone west of Monkey Mia and first zone to the north of Monkey Mia. The lightest color represents shallow water ($<$ 2 m at MSLW) and successively darker colors represent waters 2–5 m, 5–7 m, 7–9 m, and $>$ 9 m. Land is black. ∗ indicates the location of water temperature measurements. @ indicates the position of the monitoring station and the black circle represents the approximate detection range. Letters denote the habitat of zones. Several zones in deeper water contain more than one habitat (S = seagrass shoal, O = open deep water, C = channel).

Once a shark was caught, it was brought alongside a 4.5 m vessel while the drumline anchor was retrieved. To minimize stress to the shark, it was allowed to swim beside the vessel while idling forward slowly. Each shark was then measured (fork length and total length), sexed, tagged (rototag in either dorsal or pectoral fin), and released. Stomach contents were collected from dead tiger sharks and when tiger sharks regurgitated

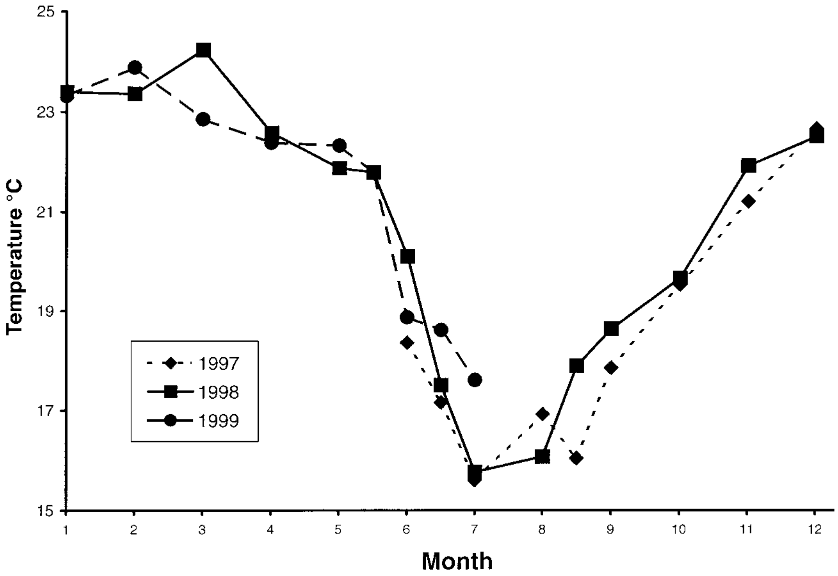

Figure 2. Water temperature in the Eastern Gulf of Shark Bay, offshore of Monkey Mia. Water temperatures during transitional months are given as two week means.

next to the boat and contents could be recovered. In most cases, it was not possible to collect all regurgitated material. However, the stomach contents were considered to be completely recorded when a tiger shark fully everted its stomach next to the boat and all contents could be recovered. Only prey items that were not fully digested (e.g. fleshy material still present) were included in analyses.

Site fidelity of tiger sharks was measured with recaptures of tagged sharks and acoustic monitoring. Between March and July 1999, five male and three female tiger sharks ($\bar{x}$ = 358 cm TL, s = 20.8) were fitted with internally implanted acoustic transmitters (V32, VEMCO, Shad Bay, NS) following the methods of Holland et al. (1999). A VR20 (VEMCO) fixed-site monitoring station, with a detection range of approximately 1.5 km (unpublished data) was deployed inside the study area (Figure 1c) for a total of 192 days (100 warm, 92 cold). Data were downloaded every 20–40 days. Based on the timing of transmitter deployments and monitoring station activity, there were 692 shark days of sampling during cold months compared to 623 during warm months. Statistical analysis of detection data treated each individual as a single data point to avoid pseudoreplication.

Seasonal changes in the relative abundance of potential prey (dugongs, sea turtles, sea snakes, and sea birds) was surveyed using belt transects. Ten transects were established in various habitats (Figure 1) and were surveyed, from a 4.5 m boat, a total of 870 times between March 1997 and July 1999 (Table 1.) All turtles and sea birds at the surface within 30 m of the vessel, dugongs within 100 m, and sea snakes (1998 and 1999 only) within 5 m were recorded. Transects were only conducted in Beaufort sea state 3 or less to reduce sighting biases associated with weather conditions.

Table 1. Number of transects surveyed.

Season	Transects
Warm 1997	101
Cold 1997	134
Warm 1998	115
Cold 1998	170
Warm 1999	194
Cold 1999	156
Total	870

Results

Fishing methods

As a result of low catch rates during June–August, analyses of fishing methods (i.e. hook size and bait portion) are restricted to sets in warmer months, when tiger shark catch rates were high. The portion of salmon used as bait (e.g. head, middle, or tail section) significantly influenced the probability of shark capture. Heads (0.39 sharks hook^{-1}) were significantly better for capturing sharks than were middle portions (0.22 sharks hook^{-1}) or tails (0.22 sharks hook^{-1}) ($\chi^2 = 18.2$, df $= 2$, $p < 0.001$). Bait retention time is probably responsible for this difference in catch rate. The average time before bait loss, on hooks that did not catch sharks, was much longer for heads ($\bar{x} = 379$ min, s $= 192$ min) than either middle ($\bar{x} = 290$ min, s $= 196$ min) or tail ($\bar{x} = 304$ min, s $= 215$ min, t $= 4.2$, df $= 506$, $p < 0.001$) sections. Bait retention times also varied seasonally. Average time until bait loss on hooks that did not capture sharks was much higher in winter ($\bar{x} = 578$ min, s $= 269$ min) than in summer ($\bar{x} = 313$ min, s $= 200$ min; t $= 16.3$, df $= 835$, $p \ll 0.001$). Fishes observed removing or feeding on baits included tiger sharks, other small sharks, *Carcharhinus* spp., guitarfish (Rhynchobatidae), schools of small teleosts, and silver toadfish, *Lagocephalus scleratus*.

Hook size significantly influenced catch rates. Corrected for bait portions used for each hook size, 12/0 hooks caught significantly fewer tiger sharks than expected while 13/0 hooks performed better than expected ($\chi^2 = 7.5$, df $= 2$, $p < 0.05$).

Tiger sharks were caught significantly more often during diurnal sets (2941 fishing hours, 181 sharks, 0.06 sharks h^{-1}) than nocturnal sets (769 hours, 22 sharks, 0.03 sharks h^{-1}; $\chi^2 = 12.1$, df $= 2$, $p < 0.001$). This trend was evident within both shallow and deep habitats.

Relative abundance, size distribution, growth, maturity, and sex ratio

A total of 252 tiger sharks were caught, and accounted for 94.4% of shark catches (n = 267). Other species of sharks were caught outside the months of peak abundance for tiger sharks (Nov–Mar), and included mako sharks, *Isurus oxyrinchus* (n = 2), silky sharks, *Carcharhinus faliciformis* (n = 2), small dusky sharks, *Carcharhinus obscurus* (n = 2), gray reef sharks, *Carcharhinus amblyrhynchos* (n = 1), nervous sharks, *Carcharhinus cautus* (n = 2), and sandbar sharks, *Carcharhinus plumbeus* (n = 6).

Tiger sharks ranged in size between 148 and 407 cm TL (Figure 3). Average female total length ($\bar{x} = 292$ cm, s $= 53$ cm, median $= 291$ cm) was smaller than that of males ($\bar{x} = 309$ cm, s $= 49$ cm, median $= 320$ cm) (t $= 2.2$, df $= 186$, $p < 0.05$). The average size of sharks was greater in warmer months ($r^2 = 0.82$, F $= 22.8$, df $= 6$, $p < 0.01$) as small sharks (< 250 cm) were caught infrequently in the warmest

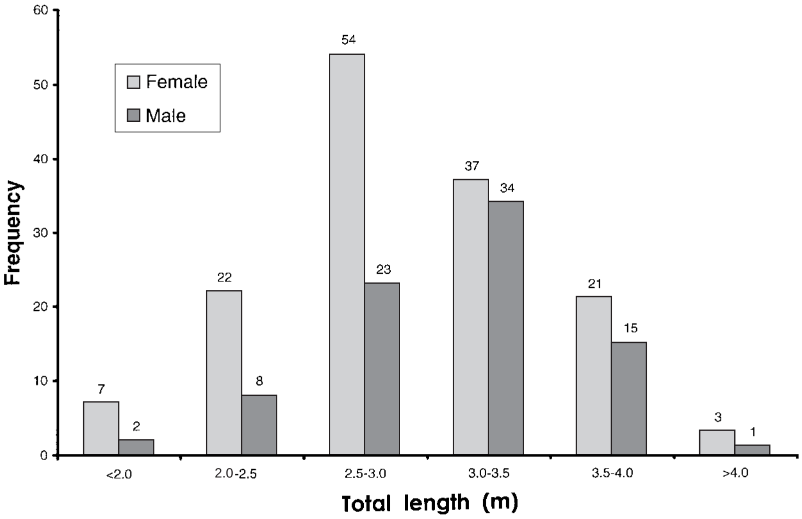

Figure 3. Size distribution of tiger sharks caught by drumline. Light bars are females and dark bars represent males. Note the skewed sex ratio of sharks under 3 m TL. Numbers above the bars represent sample size.

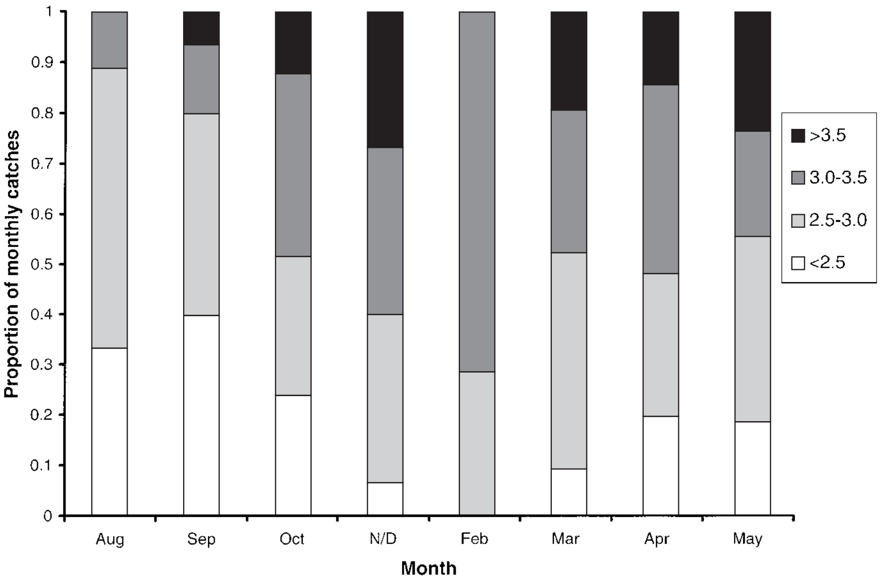

Figure 4. Seasonal changes in the relative abundance of shark size classes. The proportion of small sharks caught decreases dramatically in the warmest months. November and December data are combined due to a low sample size in December.

months (Figure 4). The largest sharks in the sample ($>$ 400 cm) were caught only during months when temperatures generally were decreasing (April and May).

Size at maturity could not be determined for females. Based on clasper calcification, males matured at approximately 300 cm TL. The smallest mature male was 298 cm while the largest immature male was 300 cm. Only seven male sharks between 290 and 305 cm were caught making a determination of precise length at maturity difficult.

Growth rates were estimated for all sharks that were recaptured (see below). Actual growth between captures and yearly growth rate estimates are given in Table 2. Although there are potential errors in the measurements, most sharks appear to grow at a rate of 20–26 cm per year. However, the only individual recaptured twice (2412) showed different growth rates during the two periods between recaptures.

The overall sex ratio observed was biased towards females (1.8 : 1; $\chi^2 = 16.8$, df $= 1$, p < 0.001), but this was mainly due to an extremely skewed sex ratio of animals under 300 cm TL (2.3 : 1, $\chi^2 = 22.3$, df $= 1$, p $\ll 0.001$). The sex ratio of sharks over 300 cm TL was not significantly different from 1:1 ($\chi^2 = 1.0$, df $=$ 1, NS). There was no significant monthly variation in overall sex ratio or sex ratio of large sharks (Chi Square Test, $\chi^2 = 6.0$, df $= 17$, NS; and $\chi^2 = 9.0$, df $= 17$, p $=$ NS, respectively).

Seasonal abundance

There were significant seasonal changes in catch rates within the study area. Tiger shark catch rate was extremely high in warm months but low from June through early August (1997/1998: $\chi^2 = 163.6$, df $=$ 10, p $\ll$ 0.001, 1999: $\chi^2 = 60.1$, df $= 5$, p $\ll$ 0.001; Figures 5, 6). However, tiger sharks were caught more often in June/July 1999 than the same period in 1997/1998 when catch rates were extremely low ($\chi^2 = 22.0$, df $= 2$, p $\ll 0.001$). In contrast, there was no significant difference in catch rates among years during warm months ($\chi^2 = 2.9$, df $= 2$, NS).

There was a significant correlation between tiger shark catch rate and water temperature (Figure 5; r $=$ 0.86, F $= 13.3$, df $= 15$, p < 0.001). Tiger shark catch rate dropped rapidly at a sea surface temperature of approximately 21–22°C in late May, and by early June 1998 (20°C), tiger sharks were almost never caught. Tiger shark catches picked up rapidly in late August, when the temperature had risen to between 16°C (1997) and 17°C (1998). Patterns of tiger shark catch rate were somewhat different in 1999. Water temperatures began to decrease in late May, as did catch rates. Despite a greater decrease in water temperature in early June, tiger sharks were still caught, although in reduced numbers. In July, the average temperature was slightly below 18°C and tiger sharks could still be caught.

Table 2. Recaptures of tiger sharks in the Eastern Gulf of Shark Bay. In the case of multiple recaptures, capture date indicates the most recent capture of a shark before recapture. TL1 = total length (cm) at capture date, TL2 = total length at recapture date. Distances are rounded to the nearest 0.5 km. There was one additional recapture of a 353 cm male in May 1998, but the tag number could not be read. (E = estimated length).

Tag	Sex	Capture	Recapture	Days	TLI (cm)	TL2 (cm)	Growth (cm)	Growth yr^{-1} (cm)	Distance (km)
2282	F	17 Mar 98	25 Mar 98	8	290	290	0	–	3.0
2296	F	13 Oct 97	19 Nov 97	37	374	–	–	–	4.5
2412	M	20 Oct 97	25 Mar 98	146	342	350	8	20	4.5
2412	M	25 Mar 98	13 Mar 99	353	350	361	11	12	3.0
3346	M	22 Oct 97	3 May 98	184	356	368	12	24	7.0
3347	M	19 Oct 97	23 Feb 99	491	280	315	35	26	1.5
3356	M	19 Oct 97	17 Mar 98	139	338	E340-350	–	–	3.5
3447	F	24 May 99	24 May 99	0.1	302	302	0	–	1.0
3490	F	15 Jun 99	26 Jun 99	11	268	269	1	–	0.5
3702	M	25 Mar 98	30 Mar 98	5	282	282	0	–	2.5
3712	F	8 Apr 98	25 Feb 99	323	299	322	23	26	3.0
3719	M	22 Apr 98	8 May 99	380	259	286	27	26	1.5
3735	F	6 May 98	19 Jun 98	44	393	394	1	–	0.0
3744	F	24 Aug 98	4 Apr 99	219	294	310	16	27	3.5
4161	M	23 Nov 97	25 Mar 98	123	351	360	9	26	3.5

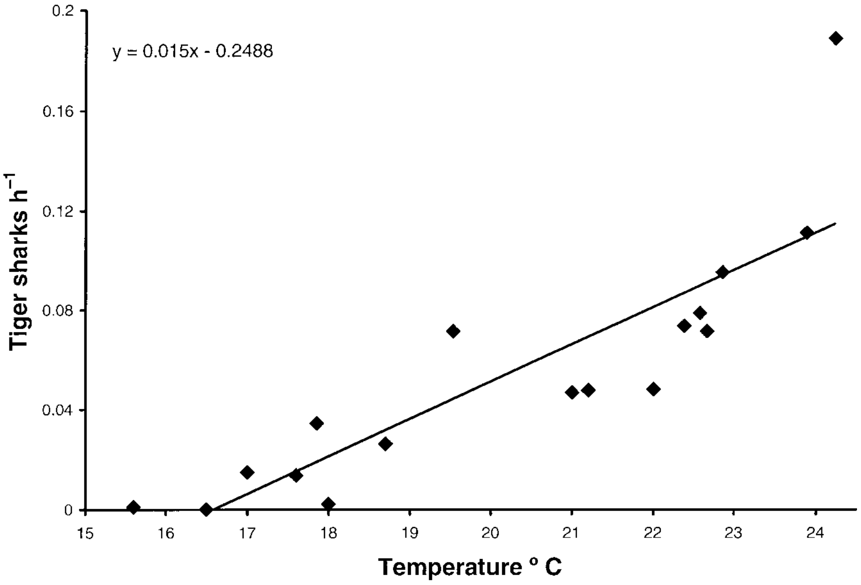

Figure 5. Correlation between water temperature and catch rate. Tiger shark catch rate is significantly influenced by water temperature ($r = 0.86$, $F = 13.3$, $df = 15$, $p < 0.001$).

Site fidelity

Sixteen tagged tiger sharks were recaptured (6.3%) within the study area after 0–491 days at liberty (Table 2). Additionally, 6 tiger sharks were recaptured that had obviously shed tags, yielding a minimum recapture rate of 8.7%. One 340 cm TL male tiger shark was recaptured ten days after release by a shark fishing vessel on an offshore coral bank (135 m depth) in the Indian Ocean (27°13.72′S, 113°6.74′E) over 150 km southwest of Monkey Mia (minimum swimming distance approximately 280–320 km). Another, female

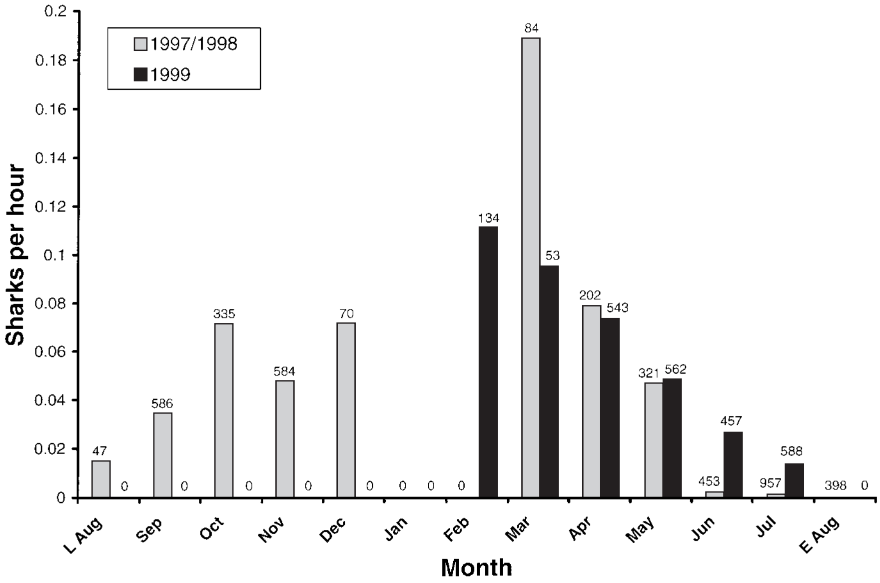

Figure 6. Seasonal changes in shark catch rates. Tiger shark abundance is very high in the warmest months of the year and lower during colder months. There is interannual variation in catch rates during cold months. Note the increase in catch rate in late August. Light bars are from 1997 and 1998. Dark bars are from 1999. Fishing hours are given above bars.

tiger shark (215 cm TL) was captured by a prawn trawler in the Western Gulf of Shark Bay (25°43′S, 113°17′E) 148 days after release.

Three male and two female tiger sharks (62.5%) fitted with internal transmitters were detected by the monitoring station after 12 to 207 days at liberty. Three sharks were detected once, one three times, and one seven times. The season of detections was not random ($\chi^2 = 13.5$, df $= 4$, $p < 0.01$) with all sharks detected during warm months. Both sharks that were detected on multiple occasions were detected at least once after an intervening cold period, as was one of the single detections.

Diet

Stomach content data were obtained for 15 sharks between 213–389 cm TL (Table 3). Complete stomach contents were obtained from four necropsies and four sharks that everted their stomachs. Dugongs were found in 7 sharks (47%), and in all sharks for which complete contents were obtained, with the exception of a 213 cm individual. However, 6 (86%) contained less than 1 kg of dugong flesh. No dugong bones were recovered. Sea snakes, primarily *Hydrophis elegans*, were the most commonly represented prey item, occurring in 9 sharks (60%), but snakes were only found in 5 sharks with complete contents (62%). Sea turtles were another commonly represented prey item, found in 4 sharks (27%). Unlike dugongs and sea snakes, turtles were only found in sharks over 299 cm, and several sharks had eaten more than one turtle. Turtle bone or shell was found in all four sharks that had consumed turtles. Teleosts (garfish, Hemirhamphidae, toadfish, Diodontidae, and unidentified fishes) were only found in the smallest shark in the sample. Elasmobranchs (black stingray, *Dasyatis thetidis,* $n = 2$ and guitarfish, Rhinobatidae, $n = 1$) were the only other prey group represented by more than one item. One tiger shark stomach contained bird remains that could not be identified to the species level.

Prey availability

The number of turtles did not vary seasonally inside the study area in 1997 ($\chi^2 = 0.4$, df $= 1$, NS) or 1998 ($\chi^2 = 2.2$, df $= 1$, NS), but in 1999, turtle density in cold months was approximately half that observed during warm months ($\chi^2 = 31.0$, df $= 1$, $p < 0.001$; Table 4). Dugongs were much more abundant in the study area during warm months in all years (1997: $\chi^2 = 58.2$, df $= 1$, $p \ll 0.001$; 1998: $\chi^2 = 93.0$, df $= 1$, $p \ll 0.001$; 1999: $\chi^2 = 41.4$, df $= 1$, $p \ll 0.001$) and were largely absent between late May and mid August

Table 3. Stomach contents of tiger sharks from the Eastern Gulf of Shark Bay. Stomach contents were obtained through either necropsies or collection of regurgitated material. Stomach contents were considered to be complete if a shark fully everted its stomach and all items could be collected. Numbers in each prey column represent the minimum number of individual prey items in each shark [C = all macroscopic stomach contents collected (Y or N), D = dugong, S = sea snake, T = sea turtle, F = teleost, B = bird, E = elasmobranch].

TL	Sex	Obtained	C	D	S	T	F	B	E	Other
213	F	Necr.	Y				4			Squid
253	F	Evert	Y	1	1					
254	F	Evert	Y	1	1					
262	M	Evert	N		1					
265	F	Evert	N		1					
273	M	Evert	N		1					
280	M	Evert	N						1	
299	F	Evert	Y	1	1	2				
303	F	Necr.	Y	1	1					
308	F	Necr.	Y	1		1		1		
314	F	Evert	N		1					
320	M	Evert	Y	1	1	1				
340	F	Evert	N							Burley
367	F	Evert	N						1	
389	F	Necr.	Y	1		2			1	

Table 4. Density (sightings km^{-2}) of tiger shark prey species.

Year	Season	Dugongs	Sea snakes	Turtles	Birds
1997	Warm	0.22	–	0.25	1.9
	Cold	0.01	–	0.23	2.7
1998	Warm	0.17	0.43	0.26	1.5
	Cold	0.005	0.01	0.27	2.4
1999	Warm	0.21	0.65	0.33	1.6
	Cold	0.06	0.15	0.16	2.1

of 1997 and 1998. Dugong abundance began to increase in late August of both years. In 1999, dugongs were present throughout the cold months and dugong density was greater than that of the cold months of 1997 and 1998 ($\chi^2 = 27.5$, df = 2, $p < 0.001$).

In 1998, sea snake abundance was high during warm months but very low during cold months ($\chi^2 = 24.5$, df = 1, $p < 0.001$; Table 4) when only one sea snake was observed (in late August). In 1999, sea snake abundance was higher in the warm months ($\chi^2 = 25.9$, df = 1, $p < 0.001$), but snakes were observed in the study area throughout June and July in densities greater than in cold months of 1998 ($\chi^2 = 12.4$, df = 1, $p < 0.001$).

Pied cormorants, *Phalacrocorax varius*, are the dominant sea birds in the study area, accounting for more than 99% of all sea bird sightings. Cormorants are found in the study area year round, but are approximately 30% more abundant during cold months (1997: $\chi^2 = 5.68$, df = 1, $p < 0.05$; 1998: $\chi^2 = 18.5$, df = 1, $p < 0.001$; 1999: $\chi^2 = 19.4$, df = 1, $p < 0.001$).

Discussion

Both hook size and type of bait had a significant influence on tiger shark catch rates. This has important implications for comparative studies of sharks as studies which employ different fishing methods may not be comparable. Also, when conducting studies across seasons or years, it is important to correct for differences in fishing methods. Shark catch rates were also significantly influenced by the time of day fishing occurred with significantly higher catches of tiger sharks during the day. The tiger shark has generally been considered nocturnal, moving inshore to feed in shallow waters at night, but these conclusions are drawn largely from anecdotal observations by fishermen (e.g. Randall 1992). Studies of tiger sharks in Hawaii suggested that small sharks feed primarily during the night, while large sharks feed at all times (Lowe et al. 1996). The present study suggests that, in Shark Bay, tiger sharks are not primarily nocturnal. Further studies will be required to determine tiger shark diel behavior.

The prevalence of large sharks caught during this study suggests that the Eastern Gulf of Shark Bay is a commonly used habitat for mature sharks of both sexes. The reason for the variation in sex ratio between small ($<$ 300 cm) and large ($>$ 300 cm) sharks is unclear. The heavy skew towards females in small size classes and an even sex ratio of larger sharks suggests that there is either differential mortality of females, compared to males, just before maturity or, more likely, there is spatial segregation of male shark size classes. Size segregation in tiger sharks has been suggested previously (Lowe et al. 1996), but this study suggests that the segregation could be sex-biased. Tiger sharks are known to cannibalize other tiger sharks (Compagno 1984), and size segregation could be due to small sharks avoiding larger sharks to minimize predation risk. However, if cannibalism were the cause for size-segregation, all juvenile sharks should avoid adults, not just males.

Site fidelity of tiger sharks is largely unknown. Several tiger sharks tagged off the coast of Florida were recaptured within 20 miles of their tagging site 1–1.5

years later (Randall 1992). In Hawaii, up to 25 % of tiger sharks tagged were found to return to the location where they had been captured previously (Holland et al. 1999). In Shark Bay, the recapture rate is lower (6–9%), but underestimates the proportion of sharks that show site fidelity as 62.5% of sharks with internal transmitters returned to the study area. The discrepancy in return rates may be due to the greater sampling efficiency of acoustic monitoring which continuously monitors for the presence of individuals in the area while fishing is conducted over a shorter time scale and requires animals to encounter baits, attack baits, and be hooked. Tiger sharks appear to show site fidelity over short and long time periods. Some individuals remain in the study area for extended periods during warm months, as four individuals were recaptured within two weeks of initial capture and 70% of detections occurred during a single warm period. Both acoustic detections and recaptures suggest that tiger sharks also return to the study area after a prolonged absence with individuals either recaptured or acoustically detected after an intervening period of cold water.

Simpfendorfer et al. (2001) found that teleosts and sea snakes were the most common prey items of tiger sharks in Shark Bay, followed by sea turtles and dugongs. This study indicates a higher frequency of occurrence of dugongs in the diet of tiger sharks. Although differences in occurrence of small prey were detected, this may be due to sampling differences (i.e. necropsy vs. predominantly regurgitation). However, the difference in the occurrence of large prey cannot be explained by sample bias, and observed differences may be largely due to differences between sample areas within Shark Bay. Simpfendorfer et al. (2001) sampled primarily in the Western Bay and in the oceanic waters bordering the bay. These areas are characterized by both rock and coral habitats while the Eastern Bay is dominated by seagrass habitats. These habitat differences probably lead to large differences in prey avaliability (e.g. dugongs and sea turtles associated with their food source, seagrass) which could explain the differences in diet within Shark Bay.

Despite the small sample size, the relative importance of dugongs in the diet of sharks is noteworthy. Most (86%) sharks contained less than a kilogram of dugong and it is unclear whether they are active predators on dugongs or if they largely scavenge carcasses. However, the availability of dugongs carcasses is likely too low to account for the high frequency of dugong occurrence in the diets of tiger sharks in both the Eastern and Western Gulf (Simpfendorfer et al. 2001), suggesting that, while tiger sharks will scavenge dugongs, they are probably also active predators.

Tiger shark predation may be important in regulating the dugong and turtle populations in Western Australia (Simpfendorfer et al. 2001), including Shark Bay. Green turtles and dugongs are seagrass grazers (e.g. Lanyon et al. 1989) and have the potential to influence the standing stock of seagrass (Preen 1995, de Iongh et al. 1995) which provides the foundation for much of the Shark Bay ecosystem (Walker 1989). Therefore, if tiger sharks influence dugong and turtle populations, it is possible that tiger sharks are a keystone predator (Paine 1966) through trophic interactions. The possibility that tiger sharks are a keystone predator in seagrass ecosystems should be a subject of future research.

Tiger shark catch rates were much higher during warm months than during cold months. This result cannot be explained by differences in bait retention time in warm and cold months as baits stayed on hooks significantly longer during winter. Analysis of the relative importance of water temperature and prey availability in determining tiger shark abundance is difficult, as seasonal trends are similar; however, neither water temperature nor overall prey availability alone adequately explains seasonal changes in tiger shark catches. A thermal constraint does not appear to be the sole determinant of tiger shark catch rates. First, several tiger sharks were captured when the water temperature (15°C) was close to the minimum recorded. Also, tiger sharks were still being caught during July 1999 when water temperatures were 2°C colder than those of June 1998 when sharks were not caught.

Overall prey availability also does not seem to explain changes in tiger shark catch rates. During the times that tiger sharks are not caught, there are still food resources present. Turtle density generally does not change seasonally and seabird abundance increases once tiger shark catch rates have decreased. Furthermore, the cold season with the highest shark catch rates (1999) was the only year in which turtle abundance declined in the cold months. However, aerial surveys by Preen et al. (1997) found that turtle density was higher in waters greater than 18°C in Shark Bay. It is possible that, although turtle density does not change in the study area, there is an increase in numbers in the Western Gulf in winter, resulting in greater food resources for tiger sharks than the Eastern Gulf.

The importance of dugongs and sea snakes in the diet of tiger sharks in Shark Bay may provide insight into the seasonal changes in shark catch rates. Changes in tiger shark catch rates closely coincide with both the departure and arrival of dugongs and sea snakes in the study area, and it is possible that tiger shark movements are in response to movements of these important, high quality prey resources. Dugongs (for large sharks) and sea snakes are probably the most energetically profitable prey items for tiger sharks in the study area. Due to differences in swimming speed and maneuverability, sea snakes probably require relatively little energy expenditure during prey capture compared to fast-swimming teleosts. Also, dugongs provide a fat-rich food source superior to turtles which require tiger sharks to ingest a large amount of indigestible material (e.g. bone and shell). During winter months, dugongs move to deeper waters north of the study area and congregate along the warmer waters of Dirk Hartog Island where there is also an abundance of turtles, teleosts, and sea snakes (Preen et al. 1997). The possibility that tiger sharks are moving in response to changes in dugong distribution is supported by a significant correlation between large dugong groups and large sharks along Dirk Hartog Island in aerial surveys of Shark Bay in winter (Anderson 1982). Further support comes from data collected in June/July 1999 when sea snakes and dugongs were still present (albeit in lower densities), and tiger sharks were caught as well.

Another possibility is that shark movements are driven by changes in prey availability in an area far removed from Shark Bay, and sharks are leaving to take advantage of a seasonally abundant resource elsewhere. Given the long distance movement of at least one Shark Bay tiger shark, this is a possibility. Future studies involving shark fishing near dugong concentrations at Dirk Hartog Island in winter, satellite tracking of tiger sharks and studies of dugong movements should shed light on the extent of shark seasonal movements and provide insight into the factors underlying them.

One critical assumption of this study is that catch rates effectively measure the abundance of tiger sharks in the study area and thus that reductions in catch rates indicate movements out of the study area. It is possible that low catch rates reflect lower feeding rates of tiger sharks rather than actual changes in abundance. Several observations independent of catches argue against this possibility. First, tiger sharks have been captured during periods of low water temperature indicating that feeding is not entirely suspended at low temperatures. Second, free-swimming tiger sharks (tagged and untagged) were only sighted during warm months. Finally, no detections were made of acoustically tagged sharks during cold months despite a larger sample. Based on these lines of evidence, there is strong support for the hypothesis that catch rates in Shark Bay are a true reflection of tiger shark abundance. Therefore, this study suggests that seasonal fluctuations in the abundance of tiger sharks in a subtropical bay are not exclusively explained by variation in water temperature, and appear to be linked to movements of high quality prey species. Also, individual sharks show site fidelity to the study area over both short and long time periods, and a large portion of sharks may use this seagrass habitat repeatedly. Future studies will be required to understand tiger shark habitat use and fine-scale movement patterns.

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